

## Hybridization of the Mexican tiger swallowtail, *Papilio alexiars garcia* (Lepidoptera: Papilionidae) with other *P. glaucus* group species and survival of pure and hybrid larvae on potential host plants

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**Abstract.** Mexican tiger swallowtails, *Papilio alexiars garcia* were collected in Nuevo Leon and Tamaulipas. Males and virgin females were hybridized with other *P. glaucus* group species. Crosses with *P. glaucus* had normal egg viability and a 1:1 sex ratio of hybrid adults. Fewer crosses with other species and subspecies were made, and the results were more variable. Inheritance of the dark female morph appeared to be the same in *P. a. garcia* as in *P. glaucus*. Pure *P. a. garcia* neonate larvae survived best on *Prunus serotina*, the natural host, and on other Rosaceae and Oleaceae with intermediate survival on species of Rutaceae, Magnoliaceae, Platanaceae, and Betulaceae. Salicaceae and Rhamnaceae species were of little value as larval hosts. In general, hybrid survival was similar but showed influences of the *P. glaucus* subspecies that was the female parent.

### Introduction

Two Mexican tiger swallowtail butterfly subspecies have been described (*Papilio alexiars alexiars* Hopffer and *P. a. garcia* Rothschild and Jordan), but little is known about their biology (Brower, 1958; Scriber, 1973; Frances & Elvira, 1978; Beutelspacher & Howe, 1984). The subspecies *P. a. alexiars* ranges throughout the states of Hidalgo, Puebla, and Veracruz, northeast of Mexico City at altitudes from 500 m to 2600 m. Both sexes are the yellow tiger-striped morph (Beutelspacher & Howe, 1984; Tyler, 1975; Jorge Llorente Bosquets, pers. comm.). *P. a. garcia* is found further to the north in Tamaulipas, Nuevo Leon, and San Luis Potosi (Fig. 1) and is reported to have only dark morph females (Beutelspacher & Howe, 1984; Lee D. Miller, pers. comm.). On the basis of male genitalia, Brower (1959) suggested that *P. alexiars* was more

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closely allied to the western species (*P. rutulus* Lucas, *P. eurymedon* Lucas, and *P. multicaudatus* Kirby) than to *P. glaucus*. L. Genetic distance data derived from allozyme electrophoresis in our laboratory support this contention (Hagen and Scriber, in prep.)

Recently, black cherry (*Prunus serotina* Ehrh.) has been observed to be one of the natural hosts of *P. a. garcia* (Evans et al., 1988; Fig 2). In this paper, we report larval acceptance and survival on various potential foodplant species used elsewhere in North America by the *Papilio glaucus* and/or *troilus* species groups. We also present data detailing various interspecific hand-pairings of *P. a. garcia* with other *Papilio glaucus* species group members. These data provide additional insights into the genetics of the dark morph female color polymorphism in the *Papilio glaucus* species group (see Clarke & Sheppard, 1959; 1962; Scriber, 1985; Scriber et al., 1986; Scriber & Evans, 1987 for discussion).

## Methods

Both male and female *P. a. garcia* were collected in Nuevo Leon and Tamaulipas, Mexico in March and April, June, and August and September 1984, 1986 and 1987. Enveloped specimens were either mailed or carried on ice to our laboratory.

Male *P. a. garcia* were hand-paired to virgin *P. a. garcia* females or virgin females of other *Papilio glaucus* group species. Field-collected and laboratory-mated females were set up in plastic boxes (10 cm × 20 cm × 27 cm) with a sprig of black cherry, *Prunus serotina*, under saturated humidity. The boxes were placed 0.7-1.0 m from continuously lighted 100 watt incandescent bulbs. Females were fed a mixture of 1 part honey to 4 parts water at least once daily. Most females were allowed to oviposit until death. After they died, hand-paired females were dissected, and the presence of spermatophores was determined. Any female not containing a spermatophore was eliminated from analysis. Field-collected females were not routinely dissected for this study because virgin *Papilio* females are rarely collected (Burns, 1968; Makielski, 1972; Pliske, 1972; Platt et al., 1984; Lederhouse & Scriber 1987a).

Eggs were collected and counted at 2-day intervals except on weekends. Larvae were removed as they hatched, and the remaining eggs were monitored for 10 days after the last larva hatched. Egg viability was the proportion of the total eggs laid that hatched as larvae. Using fine camel-hair brushes, first instar larvae (neonate) were gently placed on fresh leaves of various potential hostplants for bioassays of consumption and survival. Leaf moisture was maintained using aquapics, and fresh leaves were provided 3 times per week throughout larval development. Larval survival equaled the percent of first instars set up on a host that successfully molted to the second instar. Means were calculated with each mother considered a replicate. Some progeny of field-collected *P. a. garcia* females were used in subsequent matings.

## Results and Discussion

The pattern of oviposition of 26 field-collected and 36 hand-paired *P. a. garcia* was similar to that of the 3 *P. glaucus* subspecies (Table 1). In

general somewhat more than half of the females that were set up laid some eggs. Of those females than laid eggs, field-collected females were more likely than hand-paired females to produce larvae from their clutches ( $X^2$ ,  $p < 0.01$  in each case). The mean viability of *P. a. garcia* clutches laid by field-collected females was similar to those of comparable females of each *P. glaucus* subspecies (Lederhouse & Scriber, 1987a). There was considerable clutch to clutch variability in larval hatching.

Spermatophores were passed during hand-pairings between *P. a. garcia* males and females and other *P. glaucus* group species (Table 2).

Table 1. Oviposition characteristics of field-collected and laboratory reared and hand-mated females of *Papilio alexiarses garcia* and *P. glaucus* subspecies. A subsample of females that had laid more than 10 eggs was used to calculate mean egg viability.

Phenotype	No. females	% laying eggs	% layers with larvae	n	Egg Viability (%)	
					mean	range
<i>P. alexiarses</i>						
field	26	65.4	76.5	11	51.3	10.6–80.9
hand-paired	36	58.3	28.6	5	34.6	4.5–73.3
<i>P. g. glaucus</i>						
field	959	54.6	70.4	63	59.3	1.6–100.0
hand-paired	191	87.4	26.3	35	52.7	8.3–100.0
<i>P. g. canadensis</i>						
field	730	48.4	65.2	50	55.9	2.4–95.0
hand-paired	69	82.6	19.3	9	29.7	2.4–95.5
<i>P. g. australis</i>						
field	85	70.6	73.3	31	58.7	0.7–97.1
hand-paired	0	—	—	—	—	—

- Fig. 1. Typical habitat of *Papilio alexiarses garcia* west of Cola de Caballo, Nuevo Leon, Mexico at an elevation of about 1000 m.
- Fig. 2. Black cherry tree (*Prunus serotina*) where *P. a. garcia* larvae were collected. The tree was at about 1100 m elevation on Chipinque Mesa, Nuevo Leon, Mexico.
- Fig. 3. Adult *P. a. garcia* collected in Nuevo Leon, Mexico. A. Male dorsal and ventral, 15 April 1984. B. Female dorsal and ventral, 23 March 1985.
- Fig. 4. Representative hybrid adults from a yellow Ohio *P. g. glaucus* female and a *P. a. garcia* male (pairing 1071). A. Male dorsal and ventral. B. Female dorsal and ventral.
- Fig. 5. Representative hybrid adults from a dark Ohio *P. g. glaucus* female and the same *P. a. garcia* male (pairing 1100). A. Male dorsal and ventral. B. Female dorsal and ventral.
- Fig. 6. Larvae of *P. a. garcia* reared on black cherry. A. Neonate. B. Larva molting into the final instar found on black cherry in the field. C. Final (fifth) instar.



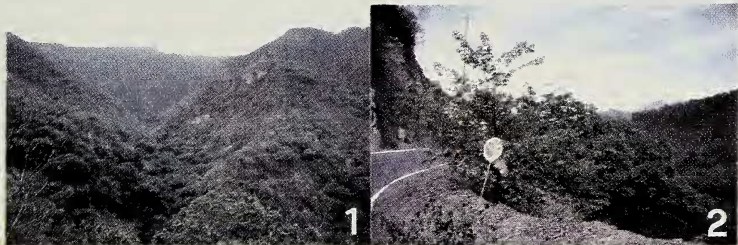




Table 2. Oviposition characteristics of *P. glaucus* species-group females hand-paired with *Papilio alexiaries garcia* males and *P. a. garcia* females hand-paired with *P. glaucus* species-group males. The female parent is listed first. Mean and range of viabilities of hybrid eggs are presented. All females were dissected, and only those containing a spermatophore are considered. Mean number of eggs and percent egg viability is presented only for females with at least one larvae.

Phenotype	Mated females	% laying eggs	% layers with larvae	Egg Mean	Egg Mean	Viability (%) Range
<i>P. g. glaucus</i> x <i>P. alexiaries</i>	24	87.5	76.2	173.9	66.1	28.4–96.9
<i>P. g. canadensis</i> x <i>P. alexiaries</i>	7	100.0	71.4	71.0	35.7	2.1–67.9
<i>P. g. australis</i> x <i>P. alexiaries</i>	6	83.3	100.0	105.8	34.8	11.5–59.1
<i>P. rutulus</i> x <i>P. alexiaries</i>	1	100.0	0.0	—	—	—
<i>P. alexiaries</i> x <i>P. g. glaucus</i>	3	100.0	33.3	15.0	60.0	—
<i>P. alexiaries</i> x <i>P. g. canadensis</i>	1	100.0	100.0	1.0	100.0	—
<i>P. alexiaries</i> x <i>P. g. australis</i>	1	100.0	100.0	21.0	9.5	—
<i>P. alexiaries</i> x <i>P. rutulus</i>	1	100.0	100.0	113.0	33.6	—
<i>P. alexiaries</i> x <i>P. eurymedon</i>	1	100.0	0.0	—	—	—

Nearly all females laid eggs. The mean viability of eggs from female *P. g. glaucus* and *P. a. garcia* males was equivalent to that of field-collected pure subspecies (Table 1). Egg viability of other hybrid crosses was lower, but not lower than that of hand-paired pure subspecies. Sex ratios at adult emergence totaled 240 males to 211 females for *P. g. glaucus* females x *P. a. garcia* males, 37:32 for *P. g. australis* females x *P. a. garcia* males, and 8:10 for *P. g. canadensis* females x *P. a. garcia* males (Table 3). None of these ratios differs significantly from an expected of 1:1 ( $X^2$ ,  $p > 0.20$  in each case). These results are further evidence of high genetic compatibility between *P. glaucus* and *P. a. garcia*.

The crosses between male *P. a. garcia* and female *P. g. glaucus* or *P. g. australis* were particularly interesting since these are the only members of the entire North American tiger swallowtail group that have dark female polymorphism (Fig. 3; Clarke & Sheppard, 1962; Scriber et al., 1987; Lederhouse & Scriber, 1987b). Our data (Table 3)

Table 3. Hybrid pairings of the two color morphs of *P. glaucus* subspecies females with *P. alexiares garcia* males and the resulting offspring. *Papilio glaucus* females were reared from mothers collected in Ohio, Illinois, Wisconsin and Florida.

Mating number	Phenotypes	Dead pupae	Males	Yellow females	Dark females
<i>P. g. glaucus</i>					
1071	Yellow OH x male 1	7	58	42	1
1072	Yellow OH x male 2	3	8	8	0
1100	Dark OH x male 1	14	61	1	49
4210	Dark OH x male 3	3	32	2	27
4211	Dark IL x male 4	7	47	2	52
4227	Dark OH x male 5	0	5	0	2
4228	Dark IL x male 6	0	5	0	5
4230	Dark IL x male 3	0	8	2	9
4234	Dark OH x male 7	0	3	0	7
4458	Dark OH x male 8	0	5	0	1
4471	Yellow OH x male 9	0	8	1	0
<i>P. g. australis</i>					
3547	Dark FL x male 10	0	27	0	27
4581	Yellow FL x male 11	1	8	3	0
4587	Yellow FL x male 12	0	1	1	0
4598	Yellow FL x male 13	0	1	1	0
<i>P. g. canadensis</i>					
1625	Yellow WI x male 14	0	0	2	0
3368	Yellow WI x male 15	0	0	1	0
4457	Yellow WI x male 16	0	2	5	0
4470	Yellow WI x male 17	1	6	2	0

suggest that the same genetic basis is likely to be involved for all 3 taxa: a Y-linked gene for melanism without color suppressors in males (Scriber, 1985; Scriber et al., 1987). Dark females (XY<sup>D</sup>) generally produce dark daughters regardless of the color of the mother of their mate, and yellow females (XY) generally only produce yellow daughters (Table 3). Occasionally, a female offspring of the opposite color from her mother will be produced (Hagen & Scriber, 1989). Possible explanations of such results are discussed elsewhere (Clarke et al. 1976, Scriber et al. 1987). Hybrid pairings of the same *P. a. garcia* male with a yellow female and a dark female produced daughters of the expected phenotype (pairing 1071, Fig. 4, pairing 1100, Fig. 5). The same pattern held for *P. g. australis* females crossed with *P. a. garcia* males (Table 3). All hybrid females from *P. g. canadensis* females crossed with *P. a. garcia* males were yellow (Table 3); *P. g. canadensis* females lack the dark gene (Scriber et al. 1987).

The newly eclosed first instar larvae of *P. a. garcia* and *P. glaucus* subspecies hybrids with *P. a. garcia* males exhibited differential survival in no-choice tests on leaves of 27 plant species from 10 plant families (Table 4). For pure *P. a. garcia*, neonates survived best on black cherry (*Prunus serotina* Ehrh.), its natural host, other *Prunus* species,







and white ash (*Fraxinus americana* L.). Intermediate levels of survival were shown by *P. a. garcia* neonates on hoptree (*Ptelea trifoliata* L., Rutaceae), tuliptree (*Liriodendron tulipifera* L., Magnoliaceae), sycamore (*Platanus occidentalis* L., Platanaceae), and paper birch (*Betula papyrifera* Marsh., Betulaceae). Although sample sizes are small in some cases, plant species in the Salicaceae and Rhamnaceae are of minimal usefulness as food plants for the Mexican tiger swallowtail. First and final instar *P. a. garcia* larvae are shown in Figure 6.

In general, hybrid survival was similar to that of pure *P. a. garcia*, but showed the influence of the particular subspecies of *P. glaucus* that was the female parent (Table 4). Hybrid survival was uniformly high on black cherry, choke cherry (*Prunus virginiana* L.), and white ash. Hybrids from *P. g. glaucus* and *P. g. australis* mothers exhibited higher survival on hosts in the families Rutaceae, Lauraceae, and Magnoliaceae. Hybrids from *P. g. canadensis* mothers had enhanced survivorship on Salicaceae hosts (Table 4).

The Magnoliaceae and Salicaceae are believed to represent major adaptive radiations in host use for North American *Papilio* from a possible Lauraceae or Rutaceae root (Scriber, 1983; 1986). Larvae of *P. g. glaucus* and *P. g. australis* readily grow on Magnoliaceae but mostly die on Salicaceae; *P. g. canadensis*, *P. rutulus*, and *P. eurymedon* larvae exhibit the opposite abilities (Lindroth et al., 1986, 1988; Scriber et al., 1986). Should *P. alexiars* represent the ancestral stock (from southwestern Pleistocene refugia) for a *P. glaucus* species group radiation, we are not surprised that *P. alexiars* larvae possess some capabilities to detoxify and process foodplants from all 4 plant families. We continue to expand our studies to assess the degree of phylogenetic affiliation of *P. alexiars garcia* with other *P. glaucus* group taxa.

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